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ZOOLOGY.

The Paroccipital of the Squamata and the Affinities of the Mosasauridae once more. A rejoinder to Professor E. D. Cope.—I. *The paroccipital.*—In 1870, Cope¹ designated the occipital externe, Cuvier, paroccipital, Owen with Huxley's name opisthotic, and homologized it with the squamosal of the Lacertilia and Ophidia. This opinion is held up in 1894 and in September, 1895,² but for the name opisthotic the name paroccipital is then used. On the other side, it is admitted by everybody else that the paroccipital, Owen (opisthotic, Huxley), which is free in the Testudines, is united with the exoccipital in the Lacertilia; the posterior portion of this bone, which is visible from behind, has been called the paroccipital process; in its anterior portion where it reaches the basioccipital it contains the posterior semicircular canals. I have stated in my last note (AM. NAT., Nov., 1895) that in young Sphenodons the paroccipital is free from the exoccipital exactly as in the Testudines and that Siebenrock has proved without question that the outer portion of the exoccipital of the Lacertilia, which lodges anteriorly the posterior semicircular canals, represents the same element. The paroccipital process of the exoccipital in Sphenodon is, of course, identical with the paroccipital process in the Lacertilia.

To this, Prof. Cope replies: "Baur asserts that the so-called parotic process [I said paroccipital process] of the exoccipital which supports the quadrate in the Squamata is the same element as that termed opisthotic by Huxley. This I deny, and believe that in this it is Baur and not myself who has fallen into error. *Siebenrock, instead of asserting this to be the case, denies it in the following language:*† 'It is not the processus paroticus of the pleurooccipital (exoccipital) which is homologous with the (paroccipital, Owen), opisthotic Huxley, but the portion anterior to the foramen nervi hypoglossi superius which protects the organ of hearing.' Siebenrock here uses the names of Owen and Huxley as referring to the same element, *but he makes the clear*

¹ Cope, E. D. On the Homologies of the Opisthotic Bone, Amer. Asso. Adv. Sc., XIX.

² Cope, E. D. On the Homologies of the posterior cranial arches in the Reptilia, Trans. Am. Philos. Soc., Vol. XVII, Apr. 27, 1892; also Am. Nat., May, 1892. The Osteology of the Lacertilia, Proc. Am. Philos. Soc., Vol. XXX, May 10, 1892, pp. 185-211. Amer. Nat., Sept. 1895, p. 855-856.

† Italics are mine.

distinction which is the important point, between the parotic process of the exoccipital and the element which contains the posterior semicircular canal.† What then is the element which articulates with the quadrate in the different orders of the Reptilia?"

The sentence quoted from Siebenrock is misleading. Siebenrock does not distinguish between the parotic process of the exoccipital and the element which contains the posterior semicircular canal. He says: *not only the parotic process but the whole portion anterior to the foramen is homologous to the paroccipital.* This whole portion, of course, contains also the parotic process. The sentence of Siebenrock translated by Cope is printed at the end of the paper in a résumé. A full account of the conditions is given on p. 209. "Die bisherige Anschauung, dass am Processus paroticus des Pleurooccipitale (exoccipitale) das Opisthoticum zu finden sei, ist daher absolut unrichtig, sondern der ganze vordere Theil des Pleurooccipitale, welche die hintere Partie des Gehörers enthält, sammt dem Processus paroticus ist als das eigentliche Paroccipitale aufzufassen."† Vergleicht man dasselbe mit dem bei den Schildkröten zeitlebens separirten Paroccipitale, so ergiebt sich schon aus der Lage und Function die Homologie der beiden Knochen." And later: "Die gleichen Verhältnisse bestehen bei Hatteria, nur bleibt bei derselben das Paroccipitale viel laenger vom Pleurooccipitale (exoccipitale) getrennt, als bei Lacerta."

That Prof. Cope has not studied Siebenrock's paper is also evident from the following sentence: "In the Testudinata, and according to Baur, in Sphenodon, the element which extends externally from the exoccipital to the quadrate is continuous with the opisthotic, but the semicircular canal is included in its proximal part only. Here the structure is entirely different from that which characterizes the Squamata, where the opisthotic does not extend distal of the canal and fuses early with the exoccipital." It is still more evident from the following words: "In the Squamata, where the opisthotic is restricted to the region of the canal and does not reach the quadrate, this so-called paroccipital is distinct." Cope thinks the paroccipital + otic portion of the paroccipital or opisthotic in the Testudines is not homologue to the paroccipital + otic portion of the paroccipital or opisthotic of the Squamata, and has the idea that this bone, paroccipital, Owen, opisthotic, Huxley. occipitale externe, Cuvier, consists of two elements, the outer one—the paroccipital—and the auditory portion, the opisthotic. He admits that "the direct evidence for such a primitive division of this element (occipital externe, Cuvier; paroccipital, Owen; opisthotic, Huxley)

† Italics are mine.

in the Testudinata has, however, yet to be produced, and I am entirely willing to give up the view above defended, should it turn out on further investigation to be untenable."

There is no further investigation necessary. The bone in question is a single element, as is shown, not only by comparative anatomy, but also by embryology. This element always is free in the Testudines; it is free in the young *Sphenodon*; and it is united with the exoccipital in the Squamata. There is not the slightest difficulty in this question.

One word about the squamosal. The squamosal of the Lacertilia and Ophidia is connected with the parietals and stands on the quadrate, outside of this element we have in the Lacertilia with well developed postorbital arch another element, which originally is united with the postorbital and is also connected with the squamosal and quadrate. This bone is the *prosquamosal*. In *Sphenodon* the squamosal and prosquamosal are united, but in the Jurassic *Saphæosaurus* (*Sauranodon*) these two elements are free as in the Lacertilia. In the Testudines the squamosal represents the squamosal of *Sphenodon*, i. e., the squamosal + prosquamosal of *Saphæosaurus* and the Lacertilia. Prof. Cope says: "the squamosal of the Squamata is homologous to the paroccipital (opisthotic, Huxley, occipital externe, Cuvier) of the Testudines. This is impossible, since the paroccipital of the Testudines is the homologue of the paroccipital process of the Lacertilia, which in front contains, exactly as in the Testudines, the posterior semicircular canals. In the *Mosasauridæ* we have the same conditions as in the generalized Lacertilia. The paroccipital and exoccipital are united; connected with the quadrate we find two elements—the inner one connected by its upper branch with the parietal process; the outer one with the postorbital. These bones are, of course, homologous to the squamosal and prosquamosal of the Lacertilia.

II. *The Affinities of the Mosasauridæ*.—Cope maintains, contrary to my statement, "that in all Lacertilia the exoccipital supports the quadrate, and that in the Pythonomorpha and the Ophidia the exoccipital does not support it or generally touch it." He also maintains "that the paroccipital (squamosal, Baur) does support the quadrate in the Ophidia, while it is only in contact with a very small part of it in the Lacertilia." I have denied in my last note that in all the Lacertilia the exoccipital supports the quadrate, and I repeat it here.

I have before me disarticulated and complete skulls of *Iguana*, *Ctenosaura*, *Amblyrhynchus* and *Conolophus*. In none of these I find an articular facet on the paroccipital (exoccipital Cope), for the

quadrate. The paroccipital even does not touch the quadrate, but is connected by the anterior and upper portion of its distal process with the inner side of the squamosal; the face of the distal end of the paroccipital is entirely free from any connection and is always visible from the outside. The paroccipital process is placed behind and also above the upper face of the quadrate for these elements. In none of the genera mentioned above I find a face on the paroccipital for the quadrate, but a face for the squamosal. In the Mosasauridæ I find the same. The quadrate is supported by the squamosal and the squamosal is connected by its inner process with the anterior face of the distal end of the paroccipital; the prosquamosal takes also part in the support of the quadrate. We have, therefore, the same conditions as in the genera mentioned. The statement that the Mosasauridæ agree with the Ophidia in the relations of the quadrate, is absolutely incorrect.—G. BAUR, University of Chicago.

EXPLANATION OF FIGURES.

Fig. 1.—*Conolophus suberistatus* Gray. Left quadrate and its relations to the squamosal, prosquamosal and paroccipital, from behind.

Fig. 2.—*Conolophus suberistatus* Gray. Left quadrate and its relations to the squamosal, prosquamosal and paroccipital, from outside and little behind.

Fig. 3.—*Conolophus suberistatus* Gray. Right quadrate and its relations to the squamosal and prosquamosal, from behind and a little inside.

Fig. 4.—*Conolophus suberistatus* Gray. Right quadrate and its relations to the squamosal and prosquamosal, from behind.

q=Quadrate.

ep=Epiphysis of quadrate.

sq=Squamosal (mastoidien, Cuvier; opisthotic, Cope, 1870; paroccipital, Cope, 1892-95).

psq=Prosquamosal (temporal, Cuvier; squamosal Cope, 1870; supratemporal, Cope, 1892-95). (Baur, G. Anat. Anz. Bd., X, p. 327.)

p=lateral process of parietals.

po=paroccipital (exoccipital, Cope).

dpo=distal end of paroccipital.

ADDITION.—After the manuscript of this note had been sent to the editor, I received the November number of the *Annals and Magazine*.

PLATE IV.

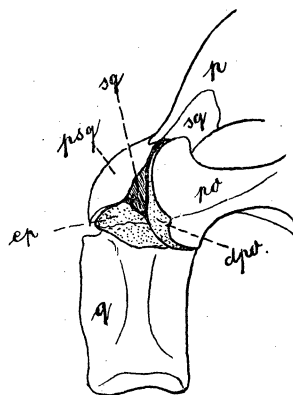


FIG. 1

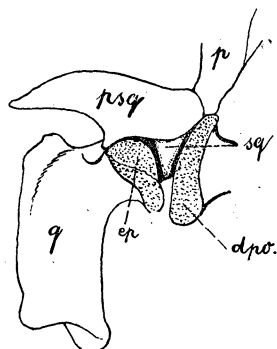


FIG. 2.

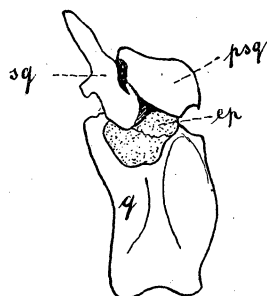


FIG. 3.

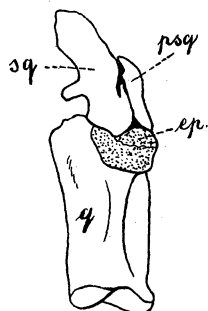


FIG. 4.

Conolophus subcristatus Gray. Quadrate and connections.

of Natural History, containing a communication of Mr. G. A. Boulenger; "Remarks on the value of certain cranial characters employed by Prof. Cope for distinguishing Lizards from Snakes." Boulenger shows also that Cope's statement, in regard to the relations of the squamosum to the quadrate of the Lacertilia, is quite incorrect.

Criticism of Dr. Baur's rejoinder on the homologies of the paroccipital bone, etc.—I. *The Paroccipital Bone.*—It seems that I have not yet made clear to Dr. Baur my position as to this element in the Reptilia. The ground for it is paleontological, and when Dr. Baur considers the question from this standpoint, he will probably find some of his very positive assumptions not proveable at present.

In the first place, we agree as to the identity in the Lacertilia, Pythonomorpha and Ophidia of the element which he calls squamosal, and which I call paroccipital. Whatever be the place of this element in the Mammalian skull, it has certainly not been proven to be the squamosal, hence I object to the name which Dr. Baur uses for it, in which position I agree with various authors. It remains to be seen whether the term paroccipital, which I have hitherto used, be appropriate. I must here repeat that at no time since 1871 have I confounded it with the opisthotic of Huxley, not even in those cases (as Testudinata) where I have supposed the two elements to be fused together.

Now the characters of this paroccipital in the Pythonomorpha are such as to suggest strongly that it represents the dismembered distal part of the paroccipito-opisthotic of the Testudinata. This character I pointed out in 1870, and it deserves more attention than it has received from Dr. Baur and other authors. It cannot be seen without taking to pieces the region to which the quadrate is articulated. When this is done it is found that the paroccipital enters as a cone between the exoccipital and petrosal, and extends inwards in Mosasaurus nearly to the region of the semicircular canals. *Nothing like this is to be found in the Lacertilia.* The question now arises, what is the meaning of this structure? As the Pythonomorpha is a cretaceous type, it is evident that it is a survival of some primitive condition, and not a derivative of the condition found in the later order of Lacertilia; where the paroccipital is entirely superficial in its connections. On the contrary, the character of the Lacertilia has been more probably derived from that of the Pythonomorpha by the loss of the proximal part of the paroccipital.

In the Testudinata the paroccipito-opisthotic has not been observed, according to Baur, to consist of two elements distinct at some stage of

embryonic life. This fact does not, however, preclude the possibility that such a division may not have existed among the ancestors of the Testudinata. As this order is very old, these ancestors can only be looked for in the Permian and Triassic periods. Characters which belong to early geologic time, are frequently dropped out of the embryonic record. Now in the Permian Reptilia, some of which are the ancestors of the Testudinata, the quadrate is a short element, and is separated from the exoccipital and the opisthotic by a separate bone which has been called mastoid and mastotympanic by Owen,³ and which I have considered as part of the "squamosal" in the absence of suture separating it from that element.⁴ I think that such an element exists in the Cotylosauria. The periotic bones in *Empedias*⁵ and *Chilonyx* are far removed from the elements which serve as suspensors of the quadrate bone, and are distinct from them in *Chilonyx* at least. Owen (l. c.) thinks that a paroccipital has been fused with the exoccipitals in *Ptychosia* (l. c.), and in a position which shows that it could not have been the opisthotic. The homologizing of one or the other of these elements with the paroccipital of the *Pythonomorpha* is too clearly among the possibilities to be negated by any evidence to the contrary yet brought forward by Dr. Baur. In fact the origin of the opisthotic element as an ossification about the posterior semicircular canal, renders it a priori probable that an osseous body at a distance from that center, such as the distal part of the paroccipitopisthotic bones in the Testudinata, was originally distinct, and for this element the name paroccipital is appropriate.

2. *The Exoccipital and Quadrate.*—Dr. Baur again denies that the exoccipital articulates with the quadrate in certain genera of *Iguanidæ* and gives some figures of that region in the *Conolophus subcristatus* to sustain his allegation. Unfortunately, though he seems to have taken the elements apart, as I suggested that he do, he did not put them together in their original relation when he had them drawn. I now give two drawings traced from the plate of the skull of the same species given by Dr. Steindachner.⁶ As these plates represent exactly the characters which I have observed and described in allied genera, I regard them as correct. It will be observed that there is a considerable contact between the exoccipital and the quadrate. There is also con-

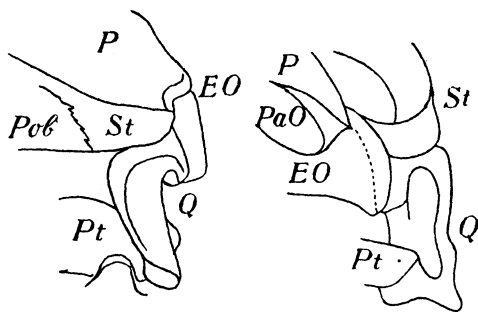
³ Proceeds. Geolog. Soc. London, 1859, p. 50.

⁴ Proceeds. Amer. Assoc. Adv. Sci., 1871, p. 207.

⁵ Proceeds. Amer. Philos. Soc., 1885, p. 236; 1895, pl. VIII, fig. 4, otic region of *Chilonyx*.

⁶ Die Schlangen u. Eidechsen der Galapagos Inseln, K. K. Zoolog. Botan. Gess. Wien, 4to. 1876; pl. V.

tact with the supratemporal, and probably with the paroccipital. *The articulation of the quadrate with the exoccipital is universal in the Iguanidæ.* I will, however, here call Dr. Baur's attention to the fact that I nowhere stated that the quadrate of the Lacertilia does not



Conolophus subcristatus Gray. From Steindachner.

touch the supratemporal or the paroccipital. I have simply asserted that the quadrate in the Lacertilia articulates with the exoccipital, and does not do so in the Ophidia. I will notice later some exceptions to the rule, of which I have since obtained information. The articulation with the supratemporal (prosquamosal, Baur) is naturally not to be mentioned in a diagnosis of the order Lacertilia, as there are numerous genera of that suborder in which that element is wanting.—E. D. COPE.

Boulanger on the Difference between Lacertilia and Ophidia; and on the Apoda.—In a recent note,⁷ Dr. Boulanger criticizes my definitions of the above suborders and the Pythonomorpha as published in a late number of this journal.⁸ He objects to the definition which I gave the Lacertilia, viz.: that the quadrate bone articulates with the exoccipital; and to that of the Ophidia, which asserts that this articulation does not take place. He suggests that I must have examined very few types of Lacertilia or I would not have made such a statement, and he mentions two or three other elements with which the quadrate bone also articulates. Now I must call Dr. Boulanger's attention to the fact that I nowhere state that the quadrate does not touch the other elements he has referred to, but have, on the contrary, stated that they do so touch. The doctor has apparently not read my article carefully, or has injected into his reading some-

⁷ *Annals and Magaz., Nat. History*, XVI, 1895, p. 367.

⁸ *AMERICAN NATURALIST*, 1895, p. 859.

thing which is not there. What he states in his note that bears on my definition is, that the quadrate in *Chlamydosaurus* does not articulate with the exoccipital, and he gives a figure to substantiate his opinion. I would have preferred to have seen a figure of this structure with the quadrate in place, but I have been able to confirm the observation by the examination of the skull of another Agamid, *Phrynocephalus olivieri*. Here the quadrate articulates with the paroccipital (supratemporal, Boul., squamosal, Baur), and is in contact with the supratemporal (squamosal, Boul.), and little or not at all with the exoccipital. How far the family of the Agamidæ generally present this structure I am unable to say, as but few skeletons of this family are at my disposal. As regards other families I have examined abundant material, as stated in my last communication (l. c., Nov. p. 1004). In review I may say that it is self evident that in general the distinction that I have drawn between Lacertilia and Ophidia in this respect is valid, (1st) because the supratemporal is frequently absent, and therefore not diagnostic; (2d) because the extremity of the paroccipital is insignificant, and affords insufficient support; (3d) because the paroccipital process of the exoccipital is the only remaining element sufficient for the purpose.

Dr. Boulenger next attacks my definition of the Ophidia, alleging that the quadrate articulates with the petrosal (proötic) or with that element and the exoccipital. Here again I am supposed to have stated that the quadrate does not articulate with the (proötic) petrosal, when in fact, I did not mention that element. As to articulation with the exoccipital, I do not consider that this can be regarded as established until the embryology and paleontology are looked into. Because an element cannot be seen in an adult skull, it does not follow that it does not exist. The paroccipital is present in the Tortricidæ, and it is, so far, only an assumption to suppose that it is not represented in the allied Uropeltidæ, and in the less allied Epanodonta and Catodonta.

The decurvature of the parietals and frontals to the basicranial axis in snakes has been cited since Müller, by Huxley,⁹ as peculiar to that order, and I know of no exceptions so far as regards the parietals. The optic foramina in some snakes with large eyes are confluent, as I have long been aware, and this foramen is at the expense of the inferior part of the frontals. This, however, does not produce the character of the Lacertilia, and the definition is not invalidated, as Dr. Boulenger alleges; nor is it by the decurvature of this bone and the parietal in the Amphisbænia, where they *do not reach* the sphenoid. I

⁹ Anatomy of Vertebrated Animals, p. 203.

did not "admit," as alleged by Boulenger that these Lacertilia "agree with the Ophidia," as they do not. Dr. Boulenger asks "what," under these circumstances, "remains of Prof. Cope's new definition of the suborders of the Squamata?" From what has preceded it is evident, first, that they are not "new" except as to the exoccipital; and second, that they remain intact, so far as any evidence to the contrary has been produced by Dr. Boulenger, except as to the articulation of the quadrate with the exoccipital in two genera of Agamidæ. And it is not necessary to observe that very few groups so closely allied as the Lacertilia and Ophidia can be defined without exceptions.

If we now look at the definitions given by Dr. Boulenger in his volumes of catalogues of lizards and of snakes in the British Museum, the necessity of something better becomes at once apparent. The Lacertilia are thus defined: "Quadrate bone articulated to the skull; parts of the ali- and orbitosphenoid regions fibrocartilaginous; rami of the mandible united by suture; temporal region without or with only one horizontal bar. Anal cleft transverse. Copulatory organs paired. *Gunther.*"

The definition of the Ophidia (dated 1893) is as follows: "Quadrate bone articulated to the skull; brain capsule entirely osseous; rami of the mandible articulated by ligament. Anal cleft transverse. Copulatory organs present paired. *Gunther.*"

In these definitions the first and last two are identical in both. The presence or absence of a horizontal bar is not definitive, and indeed no reference to it is found in the definition of the Ophidia. The only definitions left are those derived from the mode of union of the symphysis mandibuli, and the ossification of the brain case. The former of these characters is not found in several families of Lacertilia, and the latter is the one which Dr. Boulenger has repudiated in the note which gave origin to this reply. I think my attempts at definition do, in point of precision and application, compare very favorably with those which seem to have satisfied Dr. Boulenger in the work cited. In another publication he gives the characters usually employed, which are much better.

In a recent synopsis of the species of Cæciliidæ,¹⁰ Dr. Boulenger makes some observations on the relations of this family to the rest of the Urodela. He remarks: "If the absence of the limbs and reduction of the tail were the only characteristic of the group, I should, of course, not hesitate to unite the Cæcilians with the Urodeles; but, to say nothing of the scales, the Cæcilian skull presents features which are not shared by any of the tailed Batrachians, and the order can be

¹⁰ *Proceeds. Zool. Soc., London, 1895, p. 402.*

defined by the cranial characters alone. The resemblance of the larval *Ichthyophis* to *Amphiuma* is after all superficial, and although, as I believe, the *Apoda* and *Caudata* may have evolved from a common stock, *Amphiuma* is certainly not the connecting form between the two as Prof. Cope would have it, for we cannot well assume the scales, lost in the *Urodeles*, to have reappeared in the *Cæcilians*."

The above discussion is interesting but troublesome, because it requires a reply. In the first place, it ought not to be necessary to remark that the presence or absence of scales in the *Batrachia* is not an ordinal character. On the page following that from which the above is quoted, Boulenger states that six of the sixteen genera of *Apoda* (*Cæciliidæ*) *have no scales*. Further, among the extinct *Stegocephalia* some genera have scales and some have none, so there is reason to suppose that scales may be secondary as well as primary. Moreover, if a genus of salamanders should be discovered which possesses scales, no one would think of removing it from the *Urodela* on that account. There is no improbability in the supposition that such a genus may not be found in some of the Mesozoic formations. Second, Prof. Cope has never stated that the genus *Amphiuma* is the connecting form between the *Apoda* and *Caudata*. He has said that the *Amphiumoidea* probably are, and possibly the *Amphiumidæ*, but the genus *Amphiuma* never.¹ He has very rarely alleged that any genus is ancestral to any other genus. There can be no one genus between these two groups, for there is room for several genera. And one may agree with Dr. Boulenger that the *Apoda* and *Caudata* have had a common ancestor, and not disagree with the position that the *Apoda* belong to the *Caudata*, for there is no reason why that common ancestor may not probably have been one of the *Caudata*, unless there is more difference in the cranial characters of the two than has been yet pointed out.—E. D. COPE.

ENTOMOLOGY.²

Heterocera of the Lesser Antilles.—Reporting on a collection of *Geometridæ* and allied families from the islands of Grenada, St. Vincent and the Grenadines, Mr. G. F. Hampson³ says. The *Geometridæ*

¹ *Batrachia* of N. America, 1889, pp. 34-222.

² Edited by Clarence M. Weed, Durham, N. H.

³ *Ann. and Mag. Nat. Hist.*, XVI, 329.